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Racocetra intraornata, a new species in the *Glomeromycetes* with a unique spore wall structure

Bruno Tomio Goto[1*], Leonor Costa Maia[1], Gladstone Alves da Silva[1] & Fritz Oehl[2]

[1*]*brunogoto@hotmail.com*
[1]*Departamento de Micologia, CCB, Universidade Federal de Pernambuco Av. Professor Moraes Rego s/n, Cidade Universitaria, 50670-420, Recife, PE, Brazil*

[2]*Agroscope Reckenholz-Tänikon Research Station ART, Ecological Farming Systems Reckenholzstrasse 191, CH-8046 Zürich, Switzerland*

Abstract — A new species of the arbuscular mycorrhiza forming *Glomeromycetes*, with distinct ornamentations on the inner surface of the outer spore wall, is here presented under the epithet *Racocetra intraornata*. It was found in the Caatinga, a semi-arid biome of Northeastern (NE) Brazil, and also isolated from a sand dune ecosystem along the semi-humid Atlantic coast of NE Brazil. The species forms yellow to yellow-orange glomerospores, 150–280 µm in diameter, with a three-layered outer wall and a three-layered inner wall. The inner surface of the outer wall is densely crowded with small tubes that resemble germination warts characteristic of *Gigaspora*. The hyaline to rarely light yellow germination shield has 4–6 lobes and may form 4–6 germ tube initiations. The species can easily be distinguished from all other species in the *Racocetraceae* by the unique outer wall ornamentation.

Key words — *Glomeromycota*, *Gigasporineae*, *Gigasporaceae, Scutellospora*

Introduction

During studies on the diversity of arbuscular mycorrhizal fungi (AMF) in natural ecosystems of Northeastern Brazil, a new species of the *Gigasporineae* sensu Morton & Benny (1990) was found that forms bi-walled spores on sporogenous cells and a discrete, multiply lobed, hyaline to subhyaline germination shield on the inner spore wall. Species with such characteristics were recently excluded from the revised genus *Scutellospora* and re-organized in the new genus *Racocetra* of the new family *Racocetraceae* (Oehl et al. 2009). The new species has a diagnostic ornamentation on the inner surface of the outer spore wall and is hereafter described under the epithet *Racocetra intraornata*.

Material and methods

Soil sampling and culturing of AM fungi

Soils were sampled in the semi-arid Caatinga biome in the National Park of 'Vale do Catimbau' (Municipality of Buique), Pernambuco State, and in a sand dune ecosystem in Mataraca, Paraíba State, both in Northeast Brazil. The samples were taken from the rhizosphere (0–20 cm depth) of typical native plants in January 2006 (Buique) and September 2007 (Mataraca).

The site in Buique (about 700 m altitude) is situated at 08°32'54"S and 37°14'50"W, and the soil is characterized by 0.7–1.1 % organic matter, pH (H_2O) of 5.4 and 7 mg kg^{-1} available P (extracted after Mehlich; Nelson et al. 1953). The climate is semi-arid hot (type Bsh of Köppen) with a dry summer, high (30–40°C) daytime temperatures and lower (15°C) nighttime temperatures (http://prefeituradebuique.com); the mean annual precipitation is 610 mm. In this semi-arid area, Caatinga vegetation is represented by species of *Euphorbiaceae, Caesalpiniaceae, Malpighiaceae, Myrtaceae, Mimosaceae, Fabaceae,* and *Cactaceae* (e.g. *Cnidoscolus obtusifolius* Pohl, *Caesalpinia microphylla* Mart., *Byrsonima gardneriana* A. Juss., *Eugenia biflora* (L.) Dc., *Acacia bahiensis* Benth., *Bocoa mollis* (Benth.) Cowa, and *Pilosocereus tuberculatus* (Werdermann) Byles & Rowley), among others (Gomes et al. 2006).

The site in Mataraca, at 14 m altitude, is located at 06°30'00"S and 34°57'10"W, and the soil characterized by 0.7–1.1 % organic matter, pH (H_2O) of 5.5–5.8; 3–7 mg kg^{-1} P. The climate is tropical rainy (type Am of Köppen), with a short dry period of four months. The mean annual temperature is 25.5°C, and the mean annual precipitation is 1.795 mm. In the sand dune ecosystem, the vegetation is typical of 'restinga', with physiognomy varying from tree-shrub to herbaceous plants (Oliveira-Filho & Carvalho 1993). Restingas are sandy coastal plains that stand between the coastal primary sand dunes and the Brazilian Atlantic forest and thus have several plant species of both neighboring ecosystems in common. They consist of species from various families such as *Anacardiaceae, Annonaceae, Bignoniaceae, Caesalpiniaceae, Lauraceae, Myrtaceae, Rhamnaceae, Rubiaceae,* and *Sterculiaceae* (e.g. *Anacardium occidentale* L., *Caesalpinia echinata* Lam., *Eugenia kunthiana* (Kunth) Dc., *Guazuma ulmifolia* Lam., *Ocotea gardneri* (Meisn.) Mez, *Tabebuia roseoalba* (Ridl.) Sandwith, *Tapirira guianensis* Aubl., *Tocoyena selloana* Schum., *Xylopia nítida* Dunnal., and *Ziziphus joazeiro* Mart.) (Souza 2008).

The native AMF communities were cultured with *Sorghum bicolor* in 500 mL pots, filled with autoclaved sand-vermiculite substrate (1:1; w/w; 400 g per pot) mixed with the natural field soil as AMF inoculum (50 g per pot), at the greenhouse of the Department of Mycology, Universidade Federal de Pernambuco, Recife. Additionally, multiple glomerospores of the species were separated and used as infective propagules in single species cultures on *S. bicolor* (L.) Moench.The new species has not yet been propagated successfully in bait cultures or single species cultures.

Morphological analyses

Glomerospores were extracted from field soil samples and bait culture substrates by wet sieving (Gerdemann & Nicolson 1963) and sucrose centrifugation (Jenkins 1964). The spores were thereafter mounted in PVLG, PVLG + Melzer's reagent and in water,

respectively (Brundrett et al. 1994). About 100 spores were examined. In the species description, terminology followed Oehl et al. (2006), Sieverding & Oehl (2006), and Palenzuela et al. (2008) for species in the *Diversisporales* and Walker & Sanders (1986) and Oehl et al. (2009) for germination shield structures. The terminology proposed by Goto & Maia (2006) was adopted for the spore denomination.

Description of the new species

Racocetra intraornata B.T. Goto & Oehl, **sp. nov.** Figs. 1–12

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Sporocarpia ignota. Sporae singillatim in solo efformatae anguste adiacetae ad cellulas sporogeneas subterminales vel intercalares, flavae ad flavo-aurantiae, globosae (150–260 µm in diametro) vel subglobosae (145–250 × 165–280 µm); sporae cum tunicis duabus: tunica exterior stratis tribus, in totum (7.5–)9–14(–18) µm crassa, coniuncta tunicam cellulae sporogeneae et tunica hyphae; stratum exterius tunicae exterioris hyalinum, (semi-)persistens, 1.1–2.1µm crassum; stratum medium laminatum, flavum ad flavo-aurantium, 7.5–14 µm crassum, tuberculis superficie interiore altis 1.0–1.8(–2.2) µm et 0.5–1.1(–1.4) µm latis ornatum, stratum interius flavum ad flavo-aurantium, 0.5–1.3 µm crassum; stratum medium et stratum interior tunicae exterioris rubro vel rubro-brunneo colorantes reagente Melzeri; tunica interior de novo formans stratis tribus hyalinibus, in totum 3.1–4.5(–5.2) crassum; scutellum germinale in superficie exteriore tunicae interioris, hyalinum ad subhyalinum ad albo-flavum; ovale vel ellipsoidum vel rarum subglobosum, 85–125 × 60–85 µm, lobatum, paucioribus (4–6(–8)) lobis depressionibusque germinationis. Holotypus # 81–8101: URM 79247.

Type: 81–8101 (URM 79247, **holotype**) from soil samples from the semi-arid Caatinga biome in the National Park of 'Vale do Catimbau' (Municipality of Buique), Pernambuco State, Brazil.

Etymology: from the Latin: 'intra' (within, inside) and 'ornata' (ornamented) referring to the position of the tuberculate ornamentation on the inner surface of the outer spore wall.

Sporocarp formation is unknown.

Glomerospores (Figs. 1–2) formed singly in soils terminally on a subterminal or intercalary bulbous suspensor cell (= 'sporogenous' cell; Figs. 3–4). They are globose (150–260 µm in diameter) to subglobose (145–250 × 165–280 µm) to rarely irregular, bright yellow to yellow-orange, with two walls: an outer and an inner wall (ow and iw; Figs. 5–7).

Outer wall is three-layered (Fig. 5): outermost wall layer (owl1) is hyaline to subhyaline, semi-persistent to persistent, 1.1–2.1 µm thick. Second layer (owl2) is bright yellow to yellow-orange, laminate, and 7.5–14 µm thick, densely packed with tube projections on the inner surface, that are 1.0–1.8(–2.2) µm long and 0.5–1.1(–1.4) µm broad (Figs. 6–9). Tubes are about 0.6–)1.1–2.5(–3.6) µm apart from each other (Figs. 2–11). owl3 is concolorous with owl2, 0.5–1.3 µm thick, and is profiled by tube projections of owl2 (Figs. 6–9). owl2 and owl3 sometimes darken to bright orange to orange-red several months after

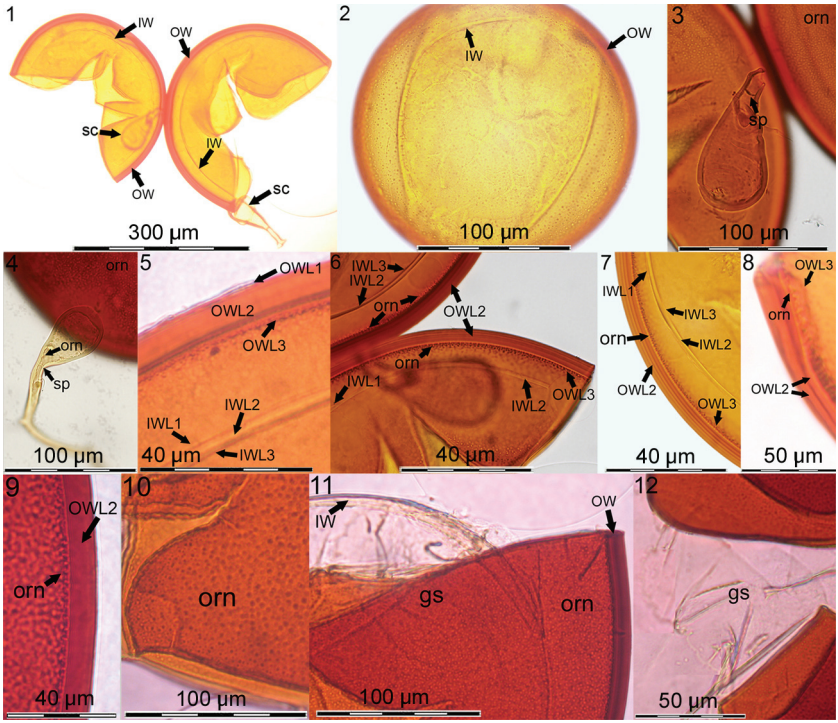
being mounted in PVLG, and both layers stain red to red-brown in Melzer's reagent (Figs. 9–12). The straight pore channel at the spore base (about 2.5–3.6 µm broad) is rarely closed by a plug formed by spore wall material of OWL2, and by OWL3, but often appears to be open.

Inner wall is three-layered (Figs. 5–7), bearing a germination shield on the outer surface (Fig. 11). Outer layer of the inner wall (IWL1) is hyaline, semi-flexible and 0.8–1.6 µm thick. Second layer (IWL2) is unit to finely laminate and 1.9–2.8 µm thick. Innermost layer (IWL3) is thin (0.4–0.8 µm thick), flexible and difficult to observe since generally tightly adherent to IWL2. The three layers do not stain in Melzer's reagent.

Sporogenous cell is subglobose to elongate, concolorous with the spore, or slightly lighter in color than the spore, and 55–85 µm long and 32–46(–56) µm broad (Figs. 1, 3–4). Two wall layers are generally visible on the sporogenous cell, continuous with OWL1 and with OWL2. OWL1 on the sporogenous cell is about 0.7–1.9 µm; adherent OWL2 is about 2.8–4.8 µm thick. The tuberculate ornamentation on OWL2 rarely continues on the wall of the sporogenous cell (Fig. 4). The pore of the sporogenous cell is generally closed at the connection to the attached 'sporogenous hypha' by a septum arising from OWL2. The sporogenous hypha generally is also bi-layered, but OWL1 is evanescent and has often sloughed off completely. In the hypha, usually 6–12(–16) additional septa, arising from OWL2, are visible in up to 150–350(–600) µm distance from the sporogenous cell. Within this distance, the sporogenous hypha tapers from 7.5–12.0 to 5.1–8.3 µm, and the hyphal wall tapers from 2.1–4.8 to 1.1–2.6 µm.

Germination shield is hyaline to subhyaline (to rarely light yellow in older spores), oval to ellipsoid (Fig. 11) or rarely subglobose, 85–125 × 60–85 µm in diameter, and have 4–6(–8) lobes (Fig. 12), that are difficult to differentiate when the shield cannot readily be observed in planar view. Irregular folds (about 5–15 µm long) arising from the shield wall separate the lobes. The one-layered shield wall and the folds are hyaline to subhyaline and generally only 0.5–1.7 µm thick. Each lobe may bear one rounded germ tube initiation (Figs. 13–14), 1.7–2.6 µm in diameter, from where the germination tubes emerge during initial germination in *Racocetra* species. The germ tube initiations, however, were difficult to detect in the specimens analyzed.

Spore development could be deduced from unequivocally identified spores found in different developmental stages in the field samples. First the outer wall differentiates a semi-persistent, unit layer (OWL1), a laminate layer with the characteristic tube projections on its inner surface (OWL2), and an adherent thin inner layer (OWL3). After the formation of one to several septa in the sporogenous hypha, separating the cell content of the spore from the hypha,



Figs. 1–12. *Racocetra intraornata*. Fig. 1. Spores with sporogenous cells (sc) attached. Fig. 2. Uncrushed spore with outer wall (ow) and inner wall (iw); round ornamentation structures visible. Figs. 3–4. Sporogenous cells with septa (sp) at the cell base. Spore wall ornamentation (orn) rarely continuing onto sc wall (Fig. 4). Figs. 5–10. Spore wall structure with three-layered outer wall (owl1-3) and three-layered inner wall (iwl1-3). Characteristic tube ornamentation (orn) on inner surface of structural, laminate layer owl2, reflected on adherent owl3. Fig. 8. owl3 separating from owl2 through strong pressure applied on cover slide; owl2 also splitting Fig. 9. Tube ornamentation on inner lamina of structural owl2 in cross view. Fig. 10. Dense tube ornamentation in planar view. Fig. 11. Hyaline germination shield on the surface of iw; lobed shield structure difficult to see in cross view. Fig. 12. Germination shield with three lobes visible. Outer wall (owl2 and owl3) staining red to red-brown in Melzer's reagent (Figs. 9–12).

the inner wall develops de novo without visible attachment to the outer wall. Finally, the lobed germination shield develops on the outer surface of the inner wall.

Auxiliary cells were not found.

Mycorrhiza formation is so far unknown.

Distribution hitherto known only from Northeastern Brazil in the semi-arid Caatinga biome (municipality Buique, Pernambuco State) and in a 'restinga'

sand dune ecosystem along the semi-humid Atlantic coast (municipality Mataraca, Paraíba State).

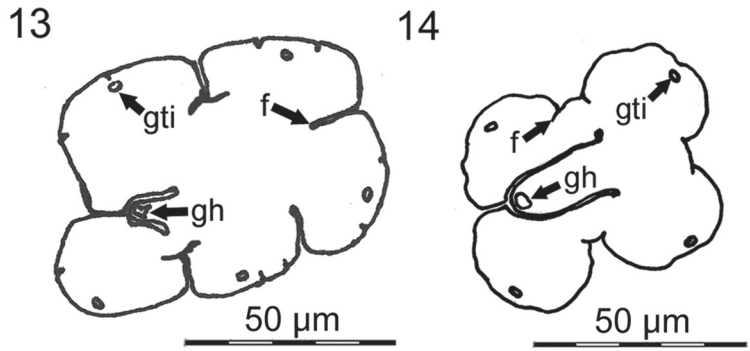
Additional specimens examined — **BRAZIL. Pernambuco State. Buique.** Isolated from soil samples from the semi-arid Caatinga biome in the National Park of 'Vale do Catimbau' (Municipality of Buique). Isotype specimens (81–8102 & 81–8103) deposited at URM (Recife, Pernambuco, Brazil). Isotypes 81–8104 & 81–8105 (OSC #134506) deposited at OSC (Corvallis, Oregon, USA). Isotypes 81–8106 & 81–8107 (ZT Myc 775) deposited at Z+ZT (Zurich, Switzerland). Other specimens from the type location area and sand dune ecosystem in Mataraca (Paraíba State) deposited at URM and at Z+ZT.

Discussion

By spore size, color and spore wall structure, and especially by the distinct ornamentation type positioned on the OWL2 inner surface tracing on OWL3 of the outer spore wall, the new species, *Racocetra intraornata*, can easily be distinguished from all other known species in the *Glomeromycetes*.

Racocetra intraornata is thus far the only species in the genus *Racocetra* with ornamentation on the inner surface of the outer wall. The nine other *Racocetra* species known so far (Oehl et al. 2009) have either no ornamentation (*R. alborosea* (Ferrer & R.A. Herrera) Oehl et al. 2009 (Ferrer & Herrera 1981), *R. castanea* (C. Walker) Oehl et al. 2009 (Walker et al. 1993), and *R. fulgida* (Koske & C. Walker) Oehl et al. 2009 and *R. weresubiae* (Koske & C. Walker) Oehl et al. 2009 (Koske & Walker 1986)), or single ornamentations positioned on the outer surface of the spore wall (*R. coralloidea* (Trappe et al.) Oehl et al. 2009 (Gerdemann & Trappe 1974), *R. gregaria* (N.C. Schenck & T.H. Nicolson) Oehl et al. 2009 (Nicolson & Schenck 1979), *R. minuta* (Ferrer & R.A. Herrera) Oehl et al. 2009 (Ferrer & Herrera 1981), and *R. persica* (Koske & C. Walker) Oehl et al. 2009 and *R. verrucosa* (Koske & C. Walker) Oehl et al. 2009 (Koske & Walker 1985)).

There are three other species in the *Gigasporineae* with a double ornamentation on the outer spore wall: *Dentiscutata nigra* (J.F. Redhead) Sieverd. et al. 2009 (Nicolson & Schenck 1979), *D. reticulata* (Koske et al.) Sieverd. et al. 2009 (Koske et al. 1983), and *D. biornata* (Spain et al.) Sieverd. et al. 2009 (Spain et al. 1989b, Oehl et al. 2009). However, the ornamentations of these species either are directed both towards the outer spore surface (in *D. nigra* and *D. reticulata*; Nicolson & Schenck 1989, Koske et al. 1983) or are positioned on the outer and inner OW surfaces, respectively (*D. biornata*; Spain et al. 1989b), while in *R. intraornata* both are equally directed on the inner OW surface (on the adherent layers OWL2 & OWL3) projecting onto smooth IW. Moreover, *D. nigra* ornamentations consist of large pits on the structural, laminated wall layer overlaying a sinuous ornamentation, and *D. reticulata* ornamentations consist of a reticulum bearing spines in the large pits of the structural layer (Nicolson & Schenck 1989, Koske et al. 1983, Oehl et al.



Figs. 13–14. *Racocetra intraornata* — drawings of germination shields in planar view. Germination shield with an initial germ hole (gh) and with several lobes each generally bearing one germ tube initiation (gti). The shield on the right appears to be more openly organized than the shield on the left, but it should be considered that the shield organization may change dependent on the pressure applied to the cover slide to make the shield more visible or to separate it from the inner wall.

2009). On the inner OW surface, only *D. biornata* has a similar fine-structured ornamentation (positioned on OWL3) as found for *R. intraornata*, but in *D. biornata* this layer easily detaches from the smooth, adherent OWL2 structural layer and consists of blunt projections, while in *R. intraornata*, OWL3 can only, if at all, be separated from the tuberculate projections of the structural OWL2 when harsh pressure is applied on the cover slide (Fig. 8). Finally, all three cited *Dentiscutata* species have significantly larger and darker colored spores than *R. intraornata* and, as typical for *Dentiscutata* species, three spore walls and conspicuous yellow-brown to brown, multiply compartmented shields with 12–30 small compartments and gti (Oehl et al. 2009).

The ornamentation on the OW inner surface in *R. intraornata* resembles germ warts of the germinal wall layer in *Gigaspora* species, but the *Gigaspora* warts are on the surface of the thin innermost layer (Spain et al. 1989a, Maia & Kimbrough 1993, Maia et al. 1994), while the *R. intraornata* tube ornamentation is on the innermost lamina of the structural layer OWL2 profiling into thin OWL3. Nevertheless, we speculate that the new species might be closely related evolutionarily to *Gigaspora* and thus possibly able to germinate not only from a germ tube initiation of the germ shield but also from the warty structure of the outer wall. This inference is not yet supported, although recent phylogenetic trees published by de Souza et al. (2005) and Sýkorová et al. (2007) do support a close evolutionary relationship between *Racocetra* spp. (e.g. *R. castanea, R. fulgida*) and *Gigaspora* spp. In this respect, our observation that all known *Gigaspora* and *Racocetra* species show a staining reaction on the outer spore wall in Melzer's reagent is noteworthy (see also Oehl et al. 2009).

Despite several attempts, the new species did not grow in bait cultures or in single species cultures. Nevertheless, we assume that *R. intraornata* form arbuscular mycorrhiza on plants without intraradical vesicle formation, as assumed for all *Diversisporales* forming spores on sporogenous cells, i.e. in the sub-order *Gigasporineae* sensu Morton & Benny (1990).

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